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Habitat selection by yellowhammers *Emberiza citrinella* on lowland farmland at two spatial scales: implications for conservation management

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Summary

1. Yellowhammer *Emberiza citrinella* populations have declined rapidly in the UK over recent decades, and a clear understanding of their habitat requirements is important to help inform conservation schemes. We aimed to disentangle and rank the effects of winter versus breeding season habitat characteristics.

2. We used information theoretic methods to analyse the factors determining yellowhammer distribution across 26 sites in England and Wales. We did this at two spatial levels: individual field boundaries and individual territories, the latter consisting of spatial clusters of boundaries.

3. We considered the role of nine predictor variables, all of which have been suggested in the literature as potentially important. These comprised boundary height and width, and the presence of hedges, trees, ditches, boundary strips, tillage crops, winter set-aside and winter stubbles.

4. The results of the statistical modelling showed that winter habitats play an important role in determining where birds locate territories in summer. In particular, the presence of rotational set-aside fields in winter showed the strongest association with summer territories.

5. There were minor differences between the territory- and boundary-based models. Most notably, the territory data demonstrated a strong preference for territories containing trees, but this was not observed in the boundary data set. We suggest that the differences between the models may reflect different scales of habitat selection. Boundary occupancy reflects broad distributions of habitat suitability; territory occupancy patterns better reveal detailed habitat requirements.

6. Regional densities were more closely correlated with the predictions of the boundary-based model than those of the territory-based model, and we discuss the implications of this for interpreting habitat association models.

7. *Synthesis and applications.* Provision of winter set-aside fields for summer territory selection by yellowhammers is an important consideration for farm management where conservation is a priority. We show that models based on occupancy of individual boundary units (e.g. hedgerows) correlate with the density of territories at the farm scale; thus farm management practices link directly to population sizes through effects on the quality of breeding habitat.

Key-words: agri-environment, Akaike weights, habitat management, metapopulation, passerines

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Introduction

Why do we find a particular animal or plant in one place as opposed to another? This question is at the core of ecology and is the focus of the large body of literature devoted to habitat selection by both animals and plants (Cody 1984; Guisan & Zimmermann 2000). More frequent occurrence in a particular habitat is usually taken to signify that this habitat is superior compared with other habitats, although there are exceptions (Van Horne 1983). Conservation managers often use such information in the preservation and restoration of habitats to help conserve populations of the animal or plant in question (Buckland & Elston 1993; Bradbury *et al*. 2000; Hinsley & Bellamy 2000; Whittingham, Percival & Brown 2000). Habitat association modelling is the common method for understanding non-random selection of a given habitat.

Boundaries surrounding fields are common throughout farmed areas in many parts of the world. Many boundaries in farmed landscapes in Europe and parts of North America consist of hedgerows, formed from linear scrub and used to enclose fields, primarily to contain livestock. Hedgerows support a diverse community of birds, often at high densities compared with other habitats such as woodland and open fields (Moore, Hooper & Davis 1967; Williamson 1971; Wyllie 1976; O'Connor 1984; Lack 1987, 1988; Cable *et al*. 1992; Fuller *et al*. 2001). Knowledge of how to manage hedgerows for birds and other wildlife is important to conservationists because many species associated with hedgerows have declined over recent decades (Siriwardena *et al*. 1998; Donald, Green & Heath 2001; Fuller *et al*. 2001). In this study we concentrated on one such species, the yellowhammer *Emberiza citrinella* L., on English farmland, and its association with habitat measured at different scales. Detailed knowledge of the habitat requirements of each farmland bird species is a key component within conservation schemes aimed at enhancing populations of farmland birds.

One of the major problems in the analysis of habitat associations is that conventional statistical methods (e.g. stepwise regression) have an inherent bias that can lead to misleading results. The problem is that model selection (i.e. deciding which regression variables should be included) is conducted at the same time as parameter inference (e.g. testing whether parameters are significantly different from zero; Miller 1990; Zhang 1992; Chatfield 1995), which can lead to biases in parameters, overfitting and incorrect significance tests. Although well known in the statistical community, this problem is commonly not appreciated in modelling applications. Multi-model inference and information theoretic approaches are increasingly recognized as a solution to these problems (Burnham & Anderson 2002).

A second problem in the analysis of habitat associations is ensuring each sampling unit is large enough to encompass the scale at which the focal animal is selecting habitat. Units such as individual boundaries (e.g. hedgerows) are convenient to measure and hence may be a more practical scale for study and prediction. However, single territories may overlap several boundaries. Therefore, the question is open as to whether analysis based on individual boundaries is representative of selection patterns at the scale of the territory. Territories are likely to be an important scale on which to measure habitat selection for birds such as yellowhammers, which actively defend territories from other individuals. Territories must include a nest site, be close to song perches and be in close proximity to food resources, because most foraging trips to collect food for the young are made within 100 m of the nest site (Morris *et al*. 2001).

One key assumption in habitat modelling is that such models apply in a broader geographical context. However, there are at least two reasons why this may not be the case. First, at low density individuals within populations may preferentially select high-quality habitat, while at high densities populations spill out into less favourable buffer habitat (Gill *et al*. 2001). Consequently, positive selection of a particular habitat component at low densities does not imply that the population cannot expand further when the most desirable habitat is fully occupied. Secondly, density-dependence may limit the expansion of populations even when the number of preferred habitat components is increased. Therefore, it is important to test whether habitat selection models are capable of predicting large-scale patterns of abundance.

In this study we used modern model selection techniques that are increasingly advocated for use in ecological modelling (Johnson & Omland 2004; Rushton, Ormerod & Kerby 2004). In addition, we used a model averaging technique giving a statistic that provides the likelihood that a predictor should appear in the best-fitting model (following Burnham & Anderson 2002). We used this approach to overcome model selection bias, to remove the arbitrariness of designating one statistical model as the best fitting model, and to construct confidence sets of models for comparing the fits of models to different data sets.

We had four main aims, to: (i) determine the factors driving habitat choice in yellowhammers, and to disentangle and rank the effects of winter vs. breeding season habitat characteristics; (ii) determine whether variables driving the selection of habitat boundaries are the same as those driving the selection of territories; (iii) determine whether local-scale habitat selection can be used to predict large-scale population density; and (iv) discuss the limitations and benefits of the statistical methods we employed.

Methods

STUDY SPECIES

We chose the yellowhammer as a study species because it is strongly associated with field boundaries (Kyrkos, Wilson & Fuller 1998; Bradbury *et al*. 2000). Survey

Table 1. List of habitat parameters used as potential explanatory predictors of yellowhammer distribution on boundaries on 26 study sites. Note: site included in all models automatically

Predictor	Description/levels	Reason for inclusion
Continuous variables		
Length of boundary	(m)	(Included in boundary model only)
Boundary height (measured for all boundary types, e.g. hedges, fences, walls, etc.)	Varies from 0 (< 1 m) to 1 (> 4 m)*	Intermediate or short boundaries preferred for territory settlement (Hinsley & Bellamy 2000)
Boundary width	Varies from 0 (< 1 m) to 1 (> 4 m)*	Wider boundaries preferred for territory settlement (Hinsley & Bellamy 2000)
Adjacent fields cropped in summer	Proportion of adjacent fields of this type (70% were autumn-sown cereal)†	Tilled fields are favoured over grassland for territory settlement and by adults foraging for their chicks (Bradbury *et al*. 2000; Hinsley & Bellamy 2000; Morris *et al*. 2001; Perkins *et al*. 2002)
Adjacent fields stubble during preceding winter	Proportion of adjacent fields of this type (all were grass leys the following summer)†	Stubble fields are strongly favoured in the winter (Wilson, Taylor & Muirhead 1996; Hancock & Wilson 2003)
Adjacent fields set-aside during preceding winter	Proportion of adjacent fields of this type (88% were rotational set-aside: of which 45% became grass fields the following summer)†	Set-aside fields are strongly favoured in the winter (Hancock & Wilson 2003; Wilson, Taylor & Muirhead 1996; Buckingham *et al*. 1999)
Categorical factors		
Site	1–26 for 26 study sites	To account for inherent differences between sites (e.g. soil type, landscape effects, etc.).
Hedge	Present/absent‡	Prefer hedges for nesting and territory settlement (Bradbury *et al*. 2000)
Ditch	Present/absent‡	Prefer ditches for nesting and territory settlement (Bradbury *et al*. 2000)
Boundary strip	Present/absent‡	Prefer boundary strips for foraging (Morris *et al*. 2001; Perkins *et al*. 2002) and territory settlement (Bradbury *et al*. 2000)
Tree presence	Present/absent‡	Trees used as song posts (Cramp & Perrins 1994)

*Each boundary was classified into five height and width categories: 1 (< 1 m), 2 (1–2 m), 3 (2–3 m), 4 (3–4 m), 5 (> 4 m). Therefore a boundary of 3 m would be scored as 0·6 in the boundary models. A territory recorded on two sampling units, one of category 1 of 100 m and the other of category 2 of 200 m, would be assigned a score of 500/1500 = 0·33. 1500 is the maximum score possible for a length of 300 m (5 × 300 m) and the actual score is 500 (1 × 100 + 2 × 200).

†Two visits to each site were made over the course of the breeding season and one visit during the winter. If no fields of a particular type were present on either side of the sampling unit (or series of sampling units for some territories) then a score of 0 was given. If all fields on both sides were of this type then a score of 1 was assigned. During the breeding season scores were averaged across both visits.

‡Note that territory-based models take an average score for these predictors (e.g. a territory recorded on three sampling units, two of which were hedges, would receive a score of 0·67 for hedges).

data were collected in 2002 from 26 sites (mean area per site, 72·94 ± 28·9 ha, 1 SD) scattered across lowland farmland in England. Each site was a farm and was part of the Common Birds Census scheme, in which voluntary observers select study areas for the scheme. Yellowhammers were surveyed on boundary sections twice per month from April to June (a minimum of six visits were made to each site, range 6–12), using Common Birds Census methods (Marchant *et al*. 1990). Boundary sections (sampling units) were defined as any contiguous length of field boundary between points of intersection with other boundaries (all boundary sections were included in the analysis irrespective of whether they were hedgerows or some other feature, e.g. fence or wall). If the nature of the boundary changed abruptly between intersections, it was further subdivided into separate sampling units.

Information was collected about the boundaries and the surrounding fields in summer 2002 (Table 1). Counts of birds were made between 07.00 and 13.00 GMT, but not in wet or windy (> force 4 on the Beaufort scale) weather. It is more difficult to see and hear birds in wet or windy conditions and fewer birds vocalize when it is raining. The locations of all individuals were mapped, and records from all censuses over the course of the visits were collated. Territories were identified from the spatiotemporal clusters of records using the methods described by Marchant *et al*. (1990). A recent continuous radio-tracking study suggests that yellowhammers are seldom recorded on field boundaries outside their territory (Jennings 2000).

LITERATURE SURVEY: MODELLING METHODS USED IN AVIAN HEDGEROW–HABITAT ASSOCIATION STUDIES

We explored the methods used to construct habitat–association models of hedgerow birds by conducting a

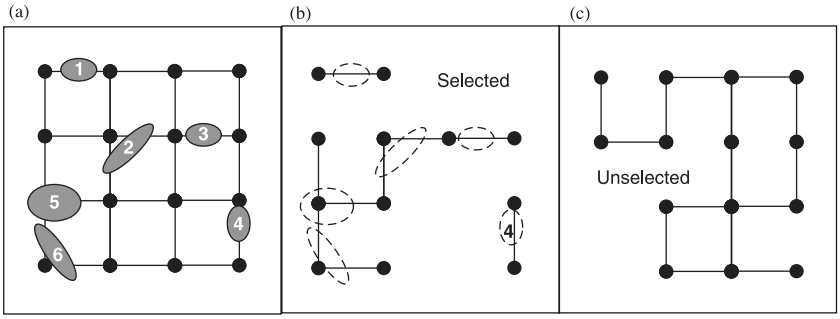


Fig. 1. (a–c) Selection of boundaries in the modelling procedure. (a) A grid of nine squares (or fields) and their boundaries upon which data from six bird territories has been overlain. At the end of the field data collection, territories were determined by clustering of records on boundary sections, e.g. all the records for territory 1 were located on one boundary. (b) Those boundaries that were selected by one or more territories. (c) Those territories that were coded as unoccupied.

literature review. The words 'boundary', 'hedgerow' and 'birds' were entered into the Web of Science database and we examined all papers that were listed and the citations within them. We deliberately excluded studies that sought to compare bird densities with other broad landscape types, such as woodland (Moore, Hooper & Davis 1967; Williamson 1971; Wyllie 1976; Lack 1987, 1988; Cable *et al*. 1992; Fuller *et al*. 2001), as we were interested in the methods used to study habitat selection patterns from sampling units that were of a similar size to that on which the animal was operating. All of the 12 avian hedgerow studies that operated at this scale treated field boundary sections as the sampling unit (Martin 1981; Arnold 1983; Osborne 1984; Rands 1986, 1987; Green, Osborne & Sears 1994; MacDonald & Johnson 1995; Parish, Lakhani & Sparks 1995; Sparks, Parish & Hinsley 1996; Bradbury *et al*. 2000; Jobin, Choinière & Bélanger 2001; Stoate & Szczur 2001). Treating each boundary as a separate replicate is likely to record the same individual birds (pair) on > 1 sampling unit because most studies are based on multiple visits (mean = 5·96 visits ± 1·21, 1 SE, assuming the mid-point when number of visits used to construct models varied) and half the studies included contiguous sampling units.

A survey of the literature revealed 9 factors that could be considered as potential predictors of yellowhammer abundance (Table 1). Some of these have been related to territory distribution (hedge presence and hedge height and width, presence of grass and tilled fields, presence of ditches and boundary strips) while others have not (winter stubble and set-aside fields and tree presence). All of the 12 studies used multiple regression techniques to identify which of a suite of candidate variables was related to bird abundance or occupancy on boundary units. Our analysis enabled us to determine the relative influence of each predictor on yellowhammer boundary and territory occupancy.

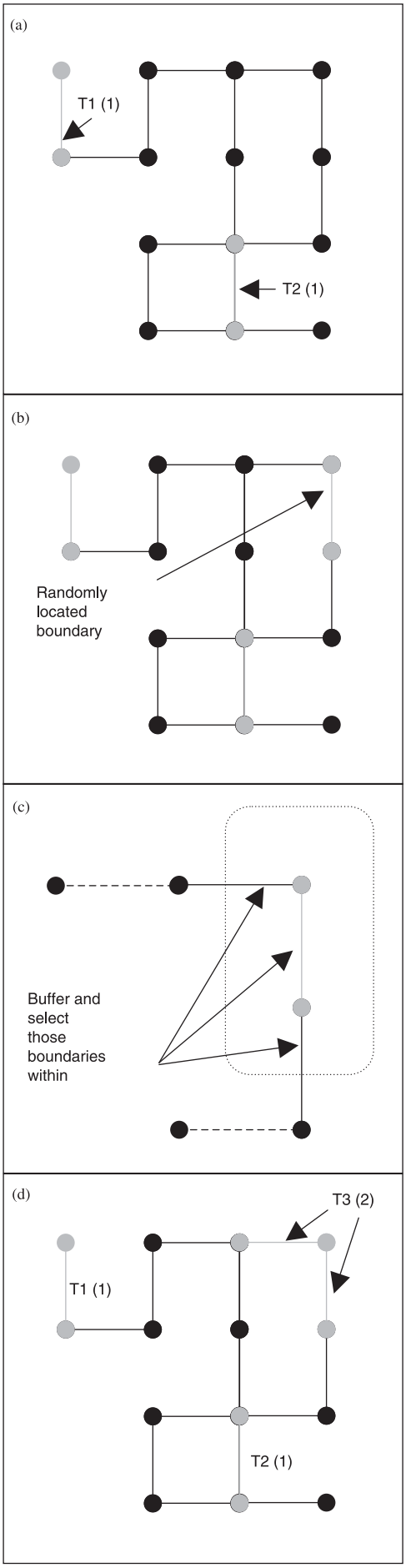
DESIGNATION OF SAMPLING UNITS

In addition to treating each sampling unit as a separate replicate in our statistical models, as is generally done (see the literature review above), we developed models based on territories (Figs 1 and 2). The territory-based models were derived using a two-stage process that sampled occupied territories (i.e. where yellowhammers were recorded during the field observations) and unoccupied 'territories' (i.e. unoccupied clusters of boundaries of similar size) separately. Spatial sampling was done in a vector GIS (Arc Info; ESRI 1998) that contained a complete spatial database of the sites. Habitat data were extracted for input to statistical software for model construction.

A territory comprised the number of boundaries that a pair occupied, not the actual size of the home range. Territories were plotted on to maps of each site, and each territory was assigned an individual code. Within the GIS, all field boundaries that were part of an occupied territory were selected and extracted from the spatial data set, leaving the remainder to be used to sample for unoccupied territories (Figs 1 and 2). Each individual territory was found to contain between one and four boundaries. We calculated one value for every predictor variable by averaging values across the boundaries within the territory. The distribution of territory sizes for each site was extracted as the number of boundaries occupied by each territory, separately for each site. This distribution drives the random sampling of the unoccupied territories described next.

For the second stage of the sampling, 'unoccupied' territories were created using a random sampling procedure constrained by the distribution of the observed territories. If N_{occ} of N_{tot} boundaries are occupied on a site, then the mean number of boundaries per territory is simply $B_t = N_{occ}/N_{terr}$, where N_{terr} is the number of territories on that site. Thus, of the N_{unocc} remaining unoccupied boundaries, the number of 'unoccupied' territories is $T_{unocc} = N_{unocc}/B_t$. The observed frequencies of boundaries per territory is $f(N)$, where $N = 0, 1, 2, 3$. Thus, the expected number of territories of size N is $T_{unocc} \times f(N)$.

Unoccupied territories were then assigned to physical locations at random, using this expected distribution of territories. However, spatial constraints were introduced to reflect constraints that limit the size of



territories. The sampling procedure ensured that unoccupied territories never included sampling units that were > 100 m apart (because we found that units separated by > 100 m were very rarely included in the same territory).

STATISTICAL METHODOLOGY

We examined correlates of variation in the probability of occurrence of yellowhammers using a generalized linear model (GLM; presence or absence of a territory along one or more sampling unit, assuming a binomial error distribution and a logit link, i.e. logistic regression). For the boundary-based model, the response variable was specified as the presence or absence of a territorial yellowhammer in a boundary section on any one census visit. For the territory-based model the response variable was specified as either an occupied territory (1) or an unoccupied territory (0).

STATISTICAL MODELLING

We used the methods described by Burnham & Anderson (2002). The approach compares the fits of a suite of candidate models using Akaike's information criterion (AIC). AIC allows models with different numbers of parameters to be directly compared with each other. If the ratio of the number of observations to number of parameters falls substantially below 40, then an adjustment should be made to the AIC to control for bias (Hurvich & Tsai 1989; Burnham & Anderson 2002). In the models reported below, the data set on territories has $n/K = 32{\cdot}8$. We therefore used the bias-adjusted AIC in the analysis of this data set.

AIC is calculated for a suite of models and the best fitting one has the smallest AIC (termed AIC_{min}). AIC differences are calculated relative to this minimum, so for model i the AIC difference (Δ_i) is calculated as:

$$\Delta_i = AIC_i - AIC_{\min}$$

The absolute size of the AIC is unimportant, instead the difference in AIC values between models indicates the relative support for the models.

CALCULATION OF AKAIKE WEIGHTS

In order to compare models we calculated Akaike weights, w_i (cf. Burnham & Anderson 2002):

Fig. 2. (a–d) Illustration of procedure used in territory-based models. (a) Two randomly selected territories each of a single boundary (T1 and T2). (b, c) Illustrating how a territory comprising two boundaries was determined. Initially a boundary was randomly selected (arrow pointing to boundary in b) and then a buffer zone of 100 m drawn around that boundary (depicted by a dotted line in c), to determine which boundaries could potentially be selected in addition to the one initially selected in (b). Of the two potential boundaries that could be selected the one running at right angles was randomly selected to produce territory T3 in (d).

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R}\exp\left(-\frac{1}{2}\Delta_r\right)} \qquad \text{eqn 1}$$

For all R models, the w_i sum to 1 and have a probabilistic interpretation: of the set of R models, w_i is the probability that model i would be selected as the best fitting model if the data were collected again under identical circumstances.

Below we report confidence sets of models fitted to each data set. A confidence set is the smallest subset of candidate models for which the w_i sum to 0·95. This represents a set of models for which we have 95% confidence that the set contains the best approximating model to the true model. It is important to note that it is not the set with 95% probability of containing the true model because we do not know that the set of models considered actually contains the true model.

Because the w_i are probabilities, it is also possible to sum these for models containing given variables (Burnham & Anderson 2002). For instance if we consider some variable k, we can calculate the sum of the Akaike weights of all the models including k, and this is the probability that, of the variables considered, variable k is in the best approximating model. This is an extremely powerful approach: it is essentially a variable selection method that considers all models, but in which each model is weighted by its plausibility.

A problem in estimating Akaike weights for individual variables is that poor predictors are not expected to have selection probabilities close to zero (Burnham & Anderson 2002). To overcome this we added a single randomly generated predictor that was uncorrelated with the response variable to the existing data set of real variables. This random predictor was generated from a uniform distribution between 0 and 1. We generated 1000 such data sets and estimated summed Akaike weights for models containing this null predictor along with the other variables.

ESTIMATION AND PREDICTION

Model averaging uses the average of parameter estimates or model predictions from each candidate model, weighted by its Akaike weight. There are a number of ways of doing this (Burnham & Anderson 2002), and we used the following methods. For parameter β_j the model-averaged estimate was calculated as:

$$\bar{\beta}_j = \sum_{i=1}^{R} w_i \hat{\beta}^{+}_{j,i} \qquad \text{eqn 2}$$

in which w_i is the Akaike weight of model i, and $\hat{\beta}^{+}_{j,i}$ is the estimate of β_j if predictor j is included in model i, or is zero otherwise. These model-averaged estimates were compared with estimates from a GLM including all variables to assess the potential impact of model selection bias on parameter estimates. The estimated selection bias for parameter j was calculated as:

$$bias_j = \left[\frac{\bar{\beta}_j - \beta_{glm}}{\bar{\beta}_j}\right] \qquad \text{eqn 3}$$

Prediction by model averaging using a set of GLM is complicated by the link function: apart from the case of the identity link function, the predicted value for a given set of predictors is not a linear function of the parameters, β. The predicted value for given data is:

$$\bar{\mu} = \sum_{i=1}^{R} w_i \hat{\mu}_i(x_i) \qquad \text{eqn 4}$$

The model-averaged prediction ($\bar{\mu}$) is the weighted average of the predicted values ($\hat{\mu}$) of the R candidate models.

MODEL FIT

We calculated an estimate of total model fit using Cohen's kappa (Fielding & Bell 1997; Fielding 1999; Manel, Williams & Ormerod 2001). This statistic compares observed occurrences and absences with those predicted by the model. To estimate this quantity, the following numbers are required: a, the number of observed occurrences that the model correctly predicts; b, the number of absences the model incorrectly predicts to be presences; c, the number of presences the model incorrectly predicts as absences; and d, the number of absences the model correctly predicts. Based on these numbers the kappa statistic may be estimated using the formula given in Fielding & Bell (1997) and Manel, Williams & Ormerod (2001).

A GLM predicts a probability of occurrence, rather then presence and absence *per se*. We therefore used two approaches to generate the above quantities. First, following Manel, Williams & Ormerod (2001), we used a cut-off threshold of predicted probability of 0·5. Predicted probabilities less than 0·5 were denoted as absences, those greater than 0·5 were denoted as presences. We denoted the estimate of the kappa statistics derived in this way as κ. Secondly, we used the predicted probabilities directly, and estimated:

$$a = \sum_{i=1}^{n^+} p_i \qquad c = n^+ - a$$
$$b = n^- - d \qquad d = \sum_{i=1}^{n^-} 1 - p_i \qquad \text{eqn 5}$$

The data are split into the n^+ and n^- cases, which are presences and absences, respectively. Then the probabilities of presences and absences are summed within these groups separately to estimate the total number of correct and incorrect predictions. We denoted the estimate of the kappa statistics derived in this way as κ′.

SET OF MODELS EXPLORED

The methods described above perform best when applied to as small a set of models as possible. Although initially our data set contained 26 possible predictors (as part of a larger project on 12 hedgerow nesting bird species), we reduced this number to 9 based on the autecology of yellowhammers and previous analyses (Table 1). We then explored all possible subsets of these 9 predictors as candidate models. Although this was a relatively large number of variables, these variables were selected based on consideration of the existing literature (Table 1). All have previously been suggested as predictors of yellowhammer abundance, and the data set could not reasonably have been reduced further. A variable coding for site was included in all models as a fixed effect (although including it as a random effect made no quantitative difference to the results), allowing large-scale variation across the sites to be controlled for in every fitted model. Although boundary length is a potentially important variable we did not include it in the analysis presented below in order to minimize the number of variables employed in the model selection. However, we found that including boundary length (to the boundary-based model) made no qualitative difference to our conclusions.

Results

MODEL SELECTION

The model selection exercise suggested that 14 models could be considered as plausible models (i.e. a 95% confidence set of models) for the boundary based data (Table 2a). These models all included hedge presence, boundary height and the presence of ditches, winter set-aside fields and boundary strips. The selection probabilities for these variables were high (> 0·98), indicating strong support. The other four variables, cropped fields (mainly cereals), boundary width, trees and winter stubble (which excluded rotational set-aside fields; Table 1), received weaker support, and the selection probabilities for these variables were well within the intervals simulated using null predictors (Table 2a). For all models the fit was very good (*c.* 0·59) when assessed using κ, although only moderate (*c.* 0·29) when assessed using κ'. We noted that the estimates of κ did not tend to correlate with the estimates of Akaike weights.

The coefficients revealed an enormous range of variation in the magnitude of the effects of the predictors on the presence of yellowhammers. All variables were measured on a scale from 0 to 1, thus the model coefficients in Table 2 measure the effect on incidence (via a logit link function) of changing from complete absence in any boundaries within the territory to presence in all of them. The ranking of the coefficients of the five variables in the model suggested as optimum is winter set-aside > boundary strip > hedge height > hedge presence > ditch presence. What is interesting about this is that the presence of territorial yellowhammers in boundaries in spring and summer appears to relate closely to winter set-aside fields: the coefficient for winter set-aside was nearly twice as large as that for hedge height and around four times as large as the coefficients for the other variables. Only two out of 17 fields (12%) that were set-aside fields in the winter (and associated with yellowhammer territories) remained as such the following summer (with almost 50% being converted to cereals or grass leys), so it seems that the presence of rotational set-aside fields in the winter is critical in determining distribution of yellowhammers. However, rotational set-aside fields are only permitted to be sprayed after 15 April and so perhaps it is the persistence of these fields at the beginning of the breeding season, as well as their presence in the winter, that is important to yellowhammers.

The models based on territories yielded broadly similar patterns (Table 2b). These models indicated that there was strong support for (in order of decreasing coefficients) the effects of winter set-aside, boundary strip presence, hedge presence, hedge height and tree presence, as indicated by high (> 0·940) selection probabilities. There was equivocal support (selection probabilities of 0·716 and 0·696) for effects of ditch presence and cropped fields. The model selection probabilities for winter stubble presence and hedge width were relatively smaller (0·278 and 0·318, respectively), and fell within the range of values simulated for null variables. Again, it is notable that the highest-ranking variable was related to winter conditions (i.e. presence of winter set-aside).

The best ranking model, in terms of the AIC, included ditch; however, the Akaike weight for this model was not appreciably larger than that of the model excluding ditch. Again, the estimates of k tended to be higher (*c.* 0·61) for κ than for κ' (0·34), and did not tend to correlate with Akaike weights. We discuss this below.

Model selection bias was large for those parameters with low selection probabilities, as would be expected (Table 2). This was true for models fitted both to the territory and boundary data. These results indicate that attempts to simplify the full model would run the risk of yielding biased parameter estimates, emphasizing the need for the approach employed here.

In total, eight models were common to the confidence sets of the two data sets, indicating that the determinants of boundary and territory occupancy are largely the same. However, the analysis of the boundary data failed to reveal the effect of tree presence.

RELATING LOCAL OCCUPANCY TO ABUNDANCE

Finally, we considered the potential use of these models to predict abundance at a larger (landscape) scale. For each of the 26 sites we generated a prediction of average boundary and territory occupancy from the boundary

Table 2. Alternative ways of deriving habitat association models based on the same data set of yellowhammer territories distributed across landscapes from 26 sites in England. All predictors from Table 1 were included in the modelling process. A fixed variable coding for site was included in all models. The table indicates the variables included in the model, the AIC, delta weight (difference between the AIC for a given model and the best fitting model) and the model selection probability (w_i). The latter are also summed for each parameter across all models by summing all w_i scores for all possible models in which the predictor was included. The null interval represents the selection probability for a randomly derived predictor obtained by 100 simulations (see text for details). Parameter estimates (β) are presented that were generated by averaging across all models (weighted by the selection probabilities). The models shown represent the 95% confidence set for each data set, models in italics are shared between the two confidence sets. Finally total model fit was assessed using Cohen's kappa statistic. This was calculated in two ways (κ and κ′), as described in the text, and measures the accuracy of prediction of occupied and unoccupied sites

Variable	Hedge	Height	Ditch	Strip	Winset	Sumtill	Width	Winstub	Trees	AIC	Δ_i	w_i	κ	κ′
(a) Models based on boundaries (n = 2443; mean occupancy = 0·26)														
AIC best	*1*	*1*	*1*	*1*	*1*	*1*				*2176·35*	*0·00*	*0·22*	0·586	0·280
	1	*1*	*1*	*1*	*1*					*2176·96*	*0·61*	*0·16*	0·588	0·279
	1	*1*	*1*	*1*	*1*	*1*	*1*			*2178·26*	*1·91*	*0·08*	0·588	0·280
	1	1	1	1	1	1		1		2178·34	1·99	0·08	0·588	0·280
	1	*1*	*1*	*1*	*1*	*1*			*1*	*2178·35*	*2·00*	*0·08*	0·586	0·280
	1	1	1	1	1		1			2178·86	2·51	0·06	0·589	0·279
	1	1	1	1	1			1		2178·93	2·58	0·06	0·588	0·279
	1	*1*	*1*	*1*	*1*				*1*	*2178·96*	*2·60*	*0·06*	0·588	0·279
	1	1	1	1	1	1	1	1		2180·25	3·90	0·03	0·590	0·280
	1	*1*	*1*	*1*	*1*	*1*	*1*		*1*	*2180·26*	*3·91*	*0·03*	0·591	0·280
	1	*1*	*1*	*1*	*1*	*1*		*1*	*1*	*2180·34*	*3·99*	*0·03*	0·588	0·280
	1	1	1	1	1		1	1		2180·84	4·48	0·02	0·589	0·279
	1	*1*	*1*	*1*	*1*		*1*		*1*	*2180·85*	*4·50*	*0·02*	0·588	0·279
	1	1	1	1	1			1	1	2180·92	4·57	0·02	0·588	0·279
Selection probability	> 0·999	> 0·999	0·989	> 0·999	0·995	0·573	0·278	0·270	0·270					
Null mean: 0·369														
Null interval: 0·269–0·654														
β	0·763	0·953	0·417	1·364	4·089	0·152	–0·021	0·018	0·002					
Bias	0·010	0·025	0·021	0·009	0·028	0·741	2·576	1·376	1·955					
(b) Models based on territories (n = 1150; mean occupancy = 0·27)														
AIC best	*1*	*1*	*1*	*1*	*1*	*1*			*1*	*1001·91*	*0·00*	*0·23*	0·613	0·340
	1	*1*	*1*	*1*	*1*				*1*	*1003·51*	*1·60*	*0·10*	0·613	0·341
	1	*1*	*1*	*1*	*1*	*1*	*1*		*1*	*1003·53*	*1·61*	*0·10*	0·623	0·337
	1	*1*		*1*	*1*	*1*			*1*	*1003·84*	*1·92*	*0·09*	0·608	0·340
	1	*1*	*1*	*1*	*1*	*1*		*1*	*1*	*1004·01*	*2·10*	*0·08*	0·612	0·336
	1	1		1	1				1	1005·12	3·21	0·05	0·615	0·337
	1	*1*	*1*	*1*	*1*		*1*		*1*	*1005·19*	*3·28*	*0·04*	0·609	0·333
	1	1	1	1	1			1	1	1005·48	3·56	0·04	0·613	0·340
	1	1		1	1	1	1		1	1005·49	3·58	0·04	0·622	0·337
Full model	1	1	1	1	1	1	1	1	1	1005·62	3·71	0·04	0·612	0·337
	1	1		1	1	1		1	1	1005·94	4·03	0·03	0·612	0·336
	1	1		1	1		1		1	1006·83	4·91	0·02	0·610	0·334
	1	1		1	1			1	1	1007·12	5·20	0·02	0·616	0·337
	1	1	1	1	1		1	1	1	1007·15	5·23	0·02	0·608	0·333
	1	1	1	1	1	1				1007·19	5·27	0·02	0·607	0·334
	1	1		1	1	1	1	1	1	1007·59	5·68	0·01	0·612	0·337
	1		1	1	1	1			1	1008·43	6·52	0·01	0·595	0·330
	1	1		1	1		1	1	1	1008·81	6·90	0·01	0·611	0·334
	1	1		1	1	1				1008·97	7·05	0·01	0·613	0·335
	1	*1*	*1*	*1*	*1*	*1*	*1*			*1009·04*	*7·13*	*0·01*	0·616	0·331
	1	*1*	*1*	*1*	*1*	*1*		*1*		*1009·30*	*7·39*	*0·01*	0·608	0·334
	1	*1*	*1*	*1*	*1*					1009·39	7·48	0·01	0·617	0·331
	1		*1*	*1*	*1*	*1*	*1*		*1*	*1009·82*	*7·90*	*0·00*	0·613	0·340
Selection probability	> 0·999	0·967	0·716	> 0·999	0·993	0·696	0·318	0·278	0·942					
Null mean: 0·368														
Interval: 0·269–0·738														
β	1·390	1·241	0·345	2·183	7·273	0·375	–0·092	0·056	0·483					
Bias	0·020	0·112	0·398	0·016	0·024	0·446	2·610	1·829	0·070					

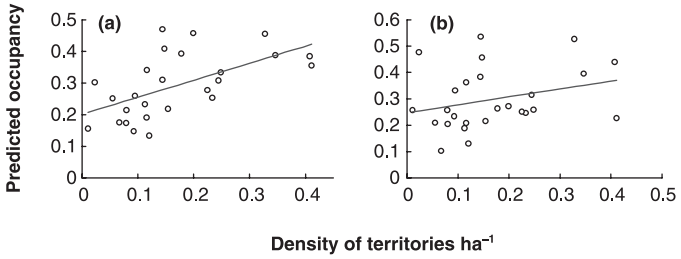


Fig. 3. Relationships between model predictions and densities of territories at each site (ha^{-1}). (a) Predictions of the model based on boundaries ($R^2 = 0{\cdot}30$, $n = 26$, $P = 0{\cdot}002$). (b) Predictions of the model based on territories ($R^2 = 0{\cdot}039$, $n = 26$, P = NS). Note that site was excluded for the list of predictors in order to generate the fitted values.

and territory-based models, respectively. We compared these with the densities of territories measured across the sites. As shown in Fig. 3, the predictions of the boundary-based model (Fig. 3a) were relatively better than those from the model based on territories (Fig. 3b). Indeed the relationship in Fig. 3b is statistically non-significant, while the relationship in Fig. 3a has moderate explanatory power ($R^2 = 0{\cdot}30$).

Discussion

One of the most useful applications of model selection procedures of the sort used here is in comparing sets of predictors between data sets, which cannot be done easily using a conventional stepwise modelling approach as this would yield a single model for each data set without indicating how much better this model is than the alternatives. Using the confidence sets we directly compared the support of models fitted to the two data sets. The results clearly indicate that the relationship between species occupancy and habitat characteristics can depend on the scale at which both are measured. By using statistical methods that allow us to quantify model selection uncertainty we have been able to demonstrate that these differences are statistically meaningful, and we have disentangled the effects of a large number of potential predictors. Two criticisms of the information theoretic approach employed here are that: (i) if the set of candidate models is poor then the resultant output will necessarily be a poor description of the data (although this is true of all modelling approaches); (ii) goodness of fit measures are required (Rushton, Ormerod & Kerby 2004). In our analysis we have dealt with these points because: (i) the set of favoured models in both analyses is small relative to the set of models considered (i.e. the 95% confidence set of models in Table 2a,b are small relative to the potential set of models); (ii) we have tested the adequacy of the models at two spatial scales, namely the boundary/territory scale, as well as the regional scale.

BOUNDARY- VS. TERRITORY-SCALE SELECTION

The boundary model can be used to predict the proportion of boundaries occupied per unit area at the farm scale (e.g. if 40 out of 100 boundaries are occupied by yellowhammers then the score in Fig. 3 would be 0·4). As this proportion is closely correlated with the density of territories in our data set ($r = 0{\cdot}86$, $n = 26$, $P < 0{\cdot}001$), the density of territories on individual farms is well predicted by the boundary model (Fig. 3a).

The predictions of the model based on territories correlate less closely with the observed density of territories (Fig. 3b). There are two differences between this model and the one based on boundaries, both relating to the aggregation of predictors at the territory scale. First, in the boundary model it was found that variables such as the presence of winter set-aside and boundary height were key variables. Much of the variation in these variables is between rather than within farms, as farms tend to have high boundaries or low ones (Kruskal–Wallis test for the effect of site on boundary height: $H = 414$, d.f. = 25, $P < 0{\cdot}001$) or either have winter non-rotational set-aside or do not (Kruskal–Wallis test for the effect of site on distribution on winter set-aside: $H = 1294$, d.f. = 25, $P < 0{\cdot}001$). In the boundary model, boundaries adjoining such features have high occupancy. However, in the territory model, most territories (whether occupied or not) on a given farm are likely to adjoin such features. These variables would then have much lower power to predict territory occupancy at the same scale as the boundary model. Secondly, it would seem likely that territories are formed in order to ensure the presence of desirable habitat components. The presence of trees was found to be a significant predictor in the territory models but not the boundary models. The presence of a tree within a territory may be important, as yellowhammers make use of them for display and song (Cramp & Perrins 1994). However, only one tree may be required per territory, and hence territories need not contain more than one boundary possessing a tree. This has the consequence that, while all territories possess trees, there may be a weaker or statistically undetectable selection for individual boundaries containing trees.

CONSEQUENCES FOR YELLOWHAMMER CONSERVATION

Our most important finding was the strong influence of winter set-aside fields on yellowhammer distribution.

Both sampling methods found set-aside fields (mainly rotational) in the previous winter to be more strongly associated with the distribution of yellowhammers than any other predictor. Previous work has linked winter field management with breeding density for a range of species (Robinson, Wilson & Crick 2001), and although yellowhammer abundance was not shown to be significantly related to winter habitats in that study, sample sizes were limited and the authors argue that such a relationship is likely to exist (Robinson, Wilson & Crick 2001). Yellowhammers are fairly sedentary, seldom being recorded > 10 km from their ringing site (Paradis *et al*. 1998), and this may explain why breeding distribution is linked to nearby wintering habitats. Carefully targeted placement of suitable wintering habitats could be beneficial for overall demography of local populations of sedentary species such as yellowhammer and corn bunting *Miliaria calandra* L. The difference in our study between the strong selection of winter set-aside fields and the lack of an association with winter stubble fields (both preferred wintering habitats) suggests that the temporal persistence of set-aside fields into the spring, in contrast to stubble fields which are often ploughed earlier in the year, may also be important.

Other predictors found to be important by both methods, namely taller hedges and boundary strips (Table 2), indicate that the effects of these two variables are well supported. The presence of ditches was found to be important using the boundary-based model but not the territory model. As the boundary-based model was found to correlate well with territory density, adding ditches is likely to increase yellowhammer density on farmland.

It is heartening that hedgerow management, ditches and boundary strips are all part of current agri-environment measures in the UK, such as the Countryside Stewardship (http://www.defra.gov.uk/erdp/schemes/css/default.htm). Several predictors, including boundary strips, ditches and hedges, have been highlighted as important to yellowhammers by a previous study aimed at identifying habitat associations at the field scale (Bradbury *et al*. 2000). Our study supports these findings but suggests both winter set-aside fields and the presence of trees are also important in determining yellowhammer settlement patterns.

SYNTHESIS AND APPLICATIONS

We found yellowhammer occupancy, as measured at two spatial scales, was most strongly associated with rotational winter set-aside field presence. This suggests that conservationists wishing to enhance local populations of yellowhammers should consider not just providing suitable habitats during the breeding season (such as boundary strips, tall hedges, ditches and trees) but also the amount and proximity of preferred wintering habitats if they wish to encourage more birds to breed during the summer. The work we have presented highlights that problems of scaling should be considered when using models for habitat selection in generating predictions for management. Specifically, we found that decisions by birds on settling territories may differ from patterns detected when analysing data from boundaries. We also found that there may be problems in extrapolating from habitat selection models based on local occupancy to regional population abundance, and this is an important potential pitfall in habitat association modelling based on presence/absence data.

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